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Darren C. Hunter[1*], Josephine M. Pemberton[2], Jill G. Pilkington[2], Michael B. Morrissey[1]

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[1] School of Biology
University of St Andrews
St Andrews
Fife
United Kingdom
KY16 9TH

[2] Institute of Evolutionary Biology
School of Biological Sciences
University of Edinburgh
Edinburgh
United Kingdom
EH9 3FL

[*] corresponding author, email: dch5@st-andrews.ac.uk

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Abstract

In nature, selection varies across time in most environments, but we lack an understanding of how specific ecological changes drive this variation. Ecological factors can alter phenotypic selection coefficients through changes in trait distributions or individual mean fitness, even when the trait-absolute fitness relationship remains constant. We apply and extend a regression-based approach in a population of Soay sheep (*Ovis aries*) and suggest metrics of environment-selection relationships that can be compared across studies. We then introduce a novel method which constructs an environmentally-structured fitness function. This allows calculation of full (as in existing approaches) and partial (acting separately through the absolute fitness function slope, mean fitness, and phenotype distribution) sensitivities of selection to an ecological variable. Both approaches show positive overall effects of density on viability selection of lamb mass. However, the second approach demonstrates that this relationship is largely driven by effects of density on mean fitness, rather than on the trait-fitness relationship slope. If such mechanisms of environmental dependence of selection are common, this could have important implications regarding the frequency of fluctuating selection, and how previous selection inferences relate to longer-term evolutionary dynamics.

Introduction

Variation in selection is key to understanding the dynamics of adaptive evolution (Bell, 2010; Uyeda *et al.*, 2011; Chevin & Haller, 2014; Estes & Arnold, 2007; Hadfield, 2016). If variation in selection occurs, any estimate from a single episode of selection, or over short timescales, will be insufficient, or potentially misleading, for predicting how that trait will evolve. While the existence and some aspects of variation in selection have been documented (Morrissey & Hadfield, 2012; Siepielski *et al.*, 2013), relating selection to environmental variables is likely to provide a much more complete picture of how and why selection varies and the likely effects on the evolutionary timescales involved (Wade & Kalisz, 1990; MacColl, 2011). However, until recently, despite many studies describing selection in natural populations (Endler, 1986; Kingsolver *et al.*, 2001), little progress has been made in understanding the ecological causes of selection (MacColl, 2011). Temporal replication provides information on how selection fluctuates over time (Morrissey & Hadfield, 2012; Siepielski *et al.*, 2009) and as a consequence provides the opportunity to investigate the importance of particular ecological factors.

Any description of selection is a representation of some aspects of a fitness landscape. This landscape relates different phenotypic or genetic combinations to population mean fitness in a given environment (Wright, 1932; Arnold, 2003). For quantitative traits, this idea can be visualised as a (potentially multi-dimensional) surface relating phenotype to fitness (Lande, 1979). The idea of a fitness landscape allows visualisation of the concept but can potentially lead to an over simplified view. For example, fitness landscapes may change as a function of environmental conditions. This has led to suggestions that the idea of a fitness landscape can be enhanced by adding extra dimensions for relevant environmental variables (Chevin *et al.*, 2010; MacColl, 2011). Key information about the fitness landscape that a population is experiencing can be gained through the calculation of fitness functions which relate individual fitness to genotype or phenotype (Arnold, 2003). Although fitness functions are central to many theoretical approaches (Geroldinger & Bürger, 2015; Slatkin, 1978), visualisations of fitness functions, or how they change in relation to changing environmental conditions are surprisingly rarely used in empirical studies (but see for e.g. Chevin *et al.*, 2015; Grant, 2002; Sinervo *et al.*, 2000).

Phenotypic selection coefficients, i.e. selection differentials (Lush, 1937; Robertson, 1966) and gradients (Lande, 1979; Lande & Arnold, 1983), provide information on the strength, shape and direction of selection on a particular trait (Phillips & Arnold, 1989) by linking relative fitness to trait values. Consequently, they have been widely used to characterise selection (Kingsolver *et al.*, 2001) and variation in selection (Morrissey & Hadfield, 2012; Siepielski *et al.*, 2013). The use of selection gradients was popularised by Lande & Arnold in their paper published in 1983 where they laid out a quantitative genetic framework for multivariate

selection analysis. In conjunction with standardising phenotype in units of standard deviations (Lande & Arnold, 1983), or less often in units of means (Hereford *et al.*, 2004), the concept of selection gradients has been critical in allowing comparisons to be made across traits, taxonomic groups etc. Specifically, this comparison is possible because phenotypic selection coefficients express the direction and strength of selection in forms that relate quantitatively to phenotypic and genetic variation, and to evolution (via the breeder's equation for differentials, and the Lande equation for gradients). These estimates provide information on the fundamental process underlying evolution by natural selection since both selection gradients and selection differentials are related to how the mean of a phenotypic trait changes due to a period of selection per unit of genetic variance (Wade & Kalisz, 1990). While phenotypic selection coefficients provide a powerful link for empirical studies of selection to evolutionary theory, the standardisations of phenotype and fitness (i.e. relative vs absolute fitness) inherent to their use, definition and comparison, makes them potentially quite distantly related to fitness functions which relate absolute fitness to unstandardised phenotypes. Many of the questions we may wish to ask about variation in selection pertain to fitness functions. Therefore, simply relating coefficients to the environment may generate incomplete representations of how the environment interacts with the trait-fitness relationships.

The fact that phenotypic selection coefficients link traits to relative rather than absolute fitness is important for the ecological interpretation of variation in selection. Whenever an estimate of relative fitness is used, it is assumed there is an underlying absolute fitness function which relates each individual's absolute fitness to its trait value in a given environment. Critically, the values of phenotypic selection coefficients are not just determined by the mean slope of this absolute fitness function. Consider selection occurring under two different sets of environmental conditions. A possible scenario is that the resulting fitness functions have the same slope in both cases, but a different mean fitness (Figure 1A). Quantification by phenotypic selection coefficients would demonstrate different trait-relative fitness relationships exist despite a very important aspect of the trait-fitness relationship (i.e., the slope) remaining constant. In fact the same may also be true for changes in the mean or variance of the trait distribution which can also affect phenotypic selection coefficients under some fitness functions. Thus, while variation in these selection coefficients alone can begin to tell us about important ways that selection varies, focussing only on phenotypic selection coefficients, without consideration of the properties of fitness functions, could obscure many ecologically important ways in which selection can vary. To this end, Chevin *et al.* (2015) constructed log-linear and Gaussian models of a fitness function and its dependence on an environmental variable. These models, based on fitting a Gaussian fitness peak, have useful and direct relationships between the model coefficients and selection gradients. However, this is a specific model and more general approaches are desirable. We hope that an additional benefit of our approach is to provide a more flexible way of modelling variation in the fitness function.

Here, we first present a simple mathematical example demonstrating that there are four different pathways through which the environment can alter phenotypic selection coefficients under a linear fitness function. We review and clarify that a change in trait mean, trait variance, mean fitness, or the relationship between the trait and fitness all can result in an altered selection differential. Variation in any (combination) of these effects could generate variation in selection. Each of these sources of variation would have very different ecological implications, which cannot be distinguished by considering variation in phenotypic selection coefficients alone, or by considering their relationship with environmental variables. Thus, no firm ecological conclusions can be drawn solely from establishing relationships between phenotypic selection coefficients and environmental variables. Standardisations of the traits and fitness required for the calculation of phenotypic selection coefficients necessarily obscure information about how environmental variables may influence fitness functions. We then develop and apply two different ways that selection in natural populations can be analysed in relation to environmental variables. Our demonstration analyses use data from an intensively studied wild population of Soay sheep (*Ovis aries*) on St Kilda, Outer Hebrides.

Our first type of analysis mirrors that which has been carried out by several other authors, where selection differentials are regressed on an environmental covariate of interest (Campbell & Powers, 2015; Husby *et al.*, 2011; Visser *et al.*, 2015) as was suggested by Wade & Kalisz (1990). This analysis introduces an important potential benefit of such an approach: the opportunity for a standardised way to quantify the effects of an environmental variable on selection that is comparable across studies, which is currently missing from the literature. Despite interest in how much selection is explained by particular aspects of ecology (e.g. McAdam & Boutin, 2003; Steele *et al.*, 2011) little has been published using a convention that would allow meaningful comparisons between studies. We suggest that a solution is to calculate the proportion of the variance seen in selection that is attributable to an environmental variable, and suggest how this can be estimated robustly in practice. In the Soay sheep, we find that a substantial amount of the variation in selection on lamb mass in August can be attributed to changes in the population size.

Next, we develop an approach based on direct estimation of an environmentally-structured fitness function i.e., the relationship between unstandardised phenotype, an environmental variable and expected absolute fitness. We also estimate the effect of an environmental variable on mean phenotype and phenotypic variance. We use these estimated functions to calculate relative fitness based selection differentials for which we can derive the total sensitivity to the environment, as well as the components of this total relationship that act through the trait-fitness relationship, mean fitness, and environment-dependent changes in the distribution of phenotype. In Soay sheep, we find that much of the dependence of selection of lamb mass on population size acts through changes in mean fitness, and that the slope of the fitness function is actually relatively constant.

Components of selection differentials

In this section the aim is to express the selection differential, S, in a way that includes the components of the underlying absolute fitness function and the trait distribution. We do this for a very simple scenario using a linear fitness function, to demonstrate the principle. This exercise highlights different pathways through which the environment can alter selection estimates and provides key information required to develop analyses assessing the individual importance of each component.

Phenotypic selection coefficients relate relative fitness, w, to a trait value, z. Relative fitness is calculated as individual absolute fitness (i.e., the response variable in a fitness function), W, divided by the mean absolute fitness,

$$w = \frac{W}{\overline{W}}. \tag{1}$$

The selection differential, S, is the change in population mean after a period of selection, $\overline{z}' - \overline{z}$. It can also be expressed as the covariance of relative fitness with the trait values (Robertson, 1966; Lande & Arnold, 1983; Lynch & Walsh, 1998),

$$S = \mathrm{cov}(w, z). \tag{2}$$

Expressing this selection coefficient in terms of an (absolute) fitness function, $W(z)$, gives

$$S = \overline{W}^{-1}\mathrm{cov}(W(z), z). \tag{3}$$

The selection differential takes into account all selection, both direct and indirect, acting on the trait (Lande & Arnold, 1983).

The direct selection gradient, β, is the average derivative of relative fitness with respect to phenotype. In multivariate analyses there is an important distinction that the selection gradient is a measure only of selection acting directly on the trait. However, in univariate form,

$$\beta = E\left[\frac{dw}{dz}\right] = \frac{\mathrm{cov}(w, z)}{\mathrm{var}(z)}. \tag{4}$$

Therefore, the difference between the two selection coefficients for univariate analyses, as we are working with here, is only in regards to scaling. The commonly used variance standardised selection gradient, β_σ, (Hereford *et al.*, 2004) is equivalent to variance standardisation of the selection differential, S/σ_z. The use and interpretation of the direct selection gradients requires more consideration when multiple traits are being considered simultaneously (Morrissey, 2014). Therefore, selection differentials are used here as we believe

144 this is a better general starting point if the methods are to later be extended to allow multivariate analysis.

145 Consider a very simple absolute fitness function, a linear function with an intercept (a) and slope (b) i.e.

$$E\left[W\right]_i = W(z) = a + bz_i. \tag{5}$$

146 Mean absolute fitness is,

$$\overline{W} = \int_{-\infty}^{+\infty} W(z)_i p(z) dz = \int_{-\infty}^{+\infty} a + bzp(z) dz = a + b\int_{-\infty}^{+\infty} zp(z) dz,$$

147 where the last term, $\int_{-\infty}^{+\infty} zp(z)dz$, is the mean phenotype, $\overline{z}$, therefore in our simple model

$$\overline{W} = a + b\overline{z}, \tag{6}$$

148 because equation (5) is a linear function.

149 The covariance of absolute fitness with the trait can be expressed as a function of the trait variance and
150 the slope of the absolute fitness function,

$$\mathrm{cov}(W, z) = b\left(E\left[z^2\right] - \left(E\left[z\right]\right)^2\right) = \sigma_z^2 b. \tag{7}$$

151 Combining equations (3), (6) and (7), the selection differential can be expressed as

$$S = \frac{\sigma_z^2 b}{a + b\overline{z}}. \tag{8}$$

152 This formula for the selection differential in terms of the parameters of a linear fitness function is useful
153 for elucidating four ways in which ecological changes could alter selection differentials and other phenotypic
154 selection coefficients. Each variable and distribution of phenotype in equation (8) represents a way through
155 which ecology can alter selection differentials. The term $b\bar{z}$ in the denominator of (8) accounts for the
156 fact that a change in mean phenotype changes mean fitness, and so ultimately S, if the fitness function is
157 sloped ($b \neq 0$). Thus, any effect of $\bar{z}$ on selection may act through changes in mean fitness, independent
158 of perturbation of a (which independently controls mean fitness). The effect of $\bar{z}$ on selection coefficients
159 is thus equivalent to the ultimate effect of one variable ($\bar{z}$) on another (S) in a path analysis, where the
160 effect is mediated by an intermediate quantity (in this case, the component of mean fitness controlled by
161 $b\bar{z}$). This pathway is distinct from, but no less ecologically relevant than, a change in a while all other
162 components remain constant. There have been implications in the literature that differences in selection

gradients (for instance among temporal or spatial replicates) attributed to environmental variables are a result of changes in trait-fitness relationships (Wade & Kalisz, 1990; MacColl, 2011). Such interpretations effectively assume all change occurs through parameter b. Almost certainly this is not the understanding of the authors themselves but it has likely led to wider belief that difference in selection gradients can be largely or solely attributed to changes in the trait fitness relationship. We hope to clarify that in fact a wider range of possible explanations exists for any change seen in a selection differential estimate and each may lead to very different ecological interpretations.

Taking the derivatives of S with respect to each of the parameters illustrates how each will change the selection differential, under this linear fitness function, when all other factors are constant. These derivatives are listed in Table (1) and depicted graphically in Figure (1). As an example, in Figure (1), doubling mean fitness from 0.4 to 0.8, while all other parameters are held constant, does not alter the absolute fitness function slope but halves the resulting variance-standardised selection gradient from 0.2 to 0.1. If only these selection gradients were reported, which is commonly the case, the information would not be available to establish that mean fitness was driving the change which could result in erroneous ecological interpretations.

The exact relationships between selection coefficients and parameters of fitness functions and phenotypic distributions will change with the nature of the fitness function and the distribution of phenotype. This may include additional pathways and higher moments, especially if fitness functions are curved (Bonamour *et al.*, 2017). However, the principles illustrated in this section should be quite general. For example, consider another simple fitness function $W(z) = a\exp(bz)$. It is well known that the selection gradient is equal to b, for this kind of fitness function, and does not depend on the value of a (Lande, 1983; Chevin *et al.*, 2015). In a situation where some ecological variable affected a, that variable would certainly be relevant to the fitness of individual organisms. Organisms experiencing high values of a would have both higher fitness, and a steeper relationship between their absolute fitness and the trait z. For this specific fitness function, these two effects cancel each other exactly i.e. an increase in a leads to a steeper relationship between z and W, this potential change in the strength of directional selection is exactly cancelled out by mean fitness itself being higher due to the increase in a. So, while neither S or β varies with a, this should not be considered a complete ecological description of the dynamic of selection. In some circumstances understanding multiple effects of a variable, such as a, on selection may be required to fully understand why selection does (or does not) vary.

Methods

Study system, data selection and handling

The Soay sheep (*Ovis aries*) of St Kilda, in the Outer Hebrides, have been the subject of an intensive individual-based long-term study since 1984 (Clutton-Brock & Pemberton, 2004). The majority of lambs within the main study area are born, caught and tagged during April each year. Each August, a large portion of the sheep, of all ages, in the study area are caught and weighed. Dates of mortality are known with high precision for the majority of individuals that use the study area through population monitoring involving 30 censuses per year, daily mortality searches of the study area during periods of high mortality (late winter), and occasional surveys of the entire island. This ensures that the lifespan of most individuals can be determined with high precision. These censuses also yield highly precise estimates of the numbers of individuals using the study area each year. Mortality, which is at least partly density-dependent, can vary dramatically between years, which results in the population size falling to very low numbers at irregular periods (Grenfell *et al.*, 1992; Clutton-Brock & Pemberton, 2004).

We investigate selection of August mass via first year survival, in relation to population size. The analyses consider the two sexes separately unless otherwise stated and use lambs which survived until the August of their first year and that were caught and measured during that August.

First year survival, our measure of absolute fitness (W), was based on census, death and capture data. Lambs were assigned as having survived the winter if they were still alive at the end of April the year after their birth. Individuals whose survival over their first winter was uncertain, 122 (10.646%) females and 188 (18.431%) males, were removed from the data set. These individuals are either known to be dead but it is not known whether or not they died prior to the end April or they have not been recorded dead but do not appear in censuses after their first winter. An alternative data set where these lambs were included and assumed to have died during their first winter was also compiled. All subsequent analyses were performed on both data sets, the results from the alternative dataset are included as a supplemental analysis (S3), but the main results reported were unchanged by the inclusion of these additional individuals.

The phenotype (z) used in the analyses was live body mass in August, measured to the nearest 0.1 kg and mean centred across all years. In cases where an individual had been captured more than once in August the entry on the day closest to the mean capture day across all 29 years, the 14^{th}, was kept. To account for growth that occurred when individuals were caught on different days throughout August the mean centred mass (z_i) was modelled against the day of August capture (Day), including year as a random effect (b_t) with

error, ϵ_i;

$$z_i = \alpha_g + b_g \text{Day} + b_t + \epsilon_i. \quad (9)$$

Males increase in mass by 0.200 kg each day during August while females gained 0.158 kg each day. These estimates were used to correct each individual's mass to that predicted for mean day of capture (the 14^{th}) in August over the 29 years. This corrects for differing capture days without removing annual differences in mass. These corrected mass estimates were used as the trait values in the following selection analyses.

The population size (E) used is representative of the core study population on the 1st of October each year, it includes all females and males seen in censuses or caught in that year and all males seen or caught before the 1^{st} of October i.e. it does not include males who only visit the study area for the rut. All lambs that were born in the study area and not subsequently recorded as dead before this date are also included in the total.

The final dataset used in the analyses included sheep born in 29 years, from 1985 to 2013. It contained 1146 female individuals and 1020 male individuals. Over this time the size of the population ranged from 211 to 672 individuals.

Regression of phenotypic selection coefficients on the environmental covariate

Possibly the simplest way that ecology can be incorporated into selection analysis builds on the idea suggested by Wade & Kalisz (1990) to estimate the covariance between, or regression of phenotypic selection coefficients on, environmental variables. By calculating selection coefficient estimates for each year individually and regressing these on the population size we quantify how selection on lamb August mass varies with population size and calculate the proportion of the variation in selection that is attributable to changing population size.

We calculated unstandardized annual selection differentials as the difference in mean trait value for individuals alive before and after the period of selection. The standard errors associated with these unstandardized selection differentials was calculated as $\sqrt{\frac{\sigma^2_{t1}}{n_{t1}} + \frac{\sigma^2_{t2}}{n_{t2}} - 2\frac{\sigma^2_{t2}}{n_{t1}}}$, where σ^2 is the variance, n is the number of individuals and the subscripts indicate whether the value is from before ($t1$) or after ($t2$) selection. Further details on this approach are provided in the supplementary material(S1). Due to small sample sizes in some years, our attempts to calculate these estimates and standard errors in other ways were unsuccessful. This was particularly true for attempts using bootstrapping to generate the standard errors, with small sample sizes inevitably some of the bootstrap samples have zero survival and therefore undefined selection differentials. This problem was unavoidable for some years when all the individuals included in the

final dataset had the same survival outcome. In these cases either a selection coefficient is undefined, if all individuals die, or the associated error cannot be calculated, if all individuals survive (due to there being no variation in the relative fitness). We therefore did not include these years in the analysis, they were generally years early in the study with very small sample sizes but also included male lambs born in 2001 when none of the 41 individuals included in our dataset survived through the winter. Additionally in some years there was only a single survivor. In these situations calculation of the standard error is complicated and any error that could be estimated would be too large to add useful information to the analysis and so these were also removed. To model the effect that the environment had on the strength of selection in each sex, we carried out regression of the selection differentials against population size taking into consideration uncertainty in the estimates. We used a diffuse inverse-gamma prior on the residual variance, using the parameters (V=1 and ν=0.002; DeVillemereuil, 2012).

$$\hat{S}_t = \mu + be_t + m_t + \epsilon_t, \tag{10}$$

where $\hat{S}_t$ is the selection differential estimate for each replicated period of selection, t, (e.g. year) and e_t is the value of the environmental variable. The measurement error associated with the selection differential estimate is included as m_t with a distribution $m_t \sim N(0, SE_t^2)$ and the residual error, ϵ_t, is distributed as $\epsilon_t \sim N(0, \sigma_\epsilon^2)$.

The variance in selection attributed to the across year variance in the environmental variable, σ_e^2, is $b^2\sigma_e^2$. While the total variance in S is

$$\sigma_S^2 = b^2\sigma_e^2 + \sigma_\epsilon^2. \tag{11}$$

The proportion of the total variation in selection attributed to the environmental component of the model is thus

$$\frac{b^2\sigma_e^2}{b^2\sigma_e^2 + \sigma_\epsilon^2}. \tag{12}$$

We can also calculate the proportion of variance in selection that would have been attributed to the environmental variable had we used a regression model which only included the point estimates of the phenotypic selection coefficients, ignoring any associated estimation error,

$$\frac{b^2\sigma_e^2}{\sigma_{\hat{S}}^2}, \tag{13}$$

where $\sigma_{\hat{S}}^2$ is the variation in the calculated selection differentials, ignoring the associated error.

Model-based full and partial sensitivities

In this section we describe the estimation of three functions which can be combined to generate model-based predictions of the selection differential, S, in any given environment, e. The sensitivity of the selection differential to changes in the environment (equivalent to the slope of the regression line in the previous section) is quantified and this sensitivity is then split into components acting through the four previously identified pathways: A change in trait mean, trait variance, mean fitness or the relationship between the trait and fitness. In order to implement the ideas demonstrated by equation (8), Table (1) and Figure (1), three functions are needed. First we need to estimate an "environmentally-structured fitness function", $W(z, e)$, linking absolute fitness to trait values, z, and the environmental variable of interest, e. We also need a function relating the mean trait value to the environmental variable, which will be denoted by $\overline{z}\,(e)$, and finally a function relating the trait variance to the environmental variable, $\sigma_z^2\,(e)$.

In order to obtain a flexible model of the effects of August mass and population density on survival, we fitted a logistic generalised linear mixed model (GLMM; Bolker *et al.*, 2009; Hadfield, 2010) assuming a binomial error distribution, $W \sim B(E[W])$, with linear and quadratic effects of mass and density, plus their interactions. We included a random effect of year. Additionally we modelled effects of sex on all terms, i.e. a main effect of sex on the model intercept, and interactions of sex with all other terms. While we subsequently conduct all analyses separately by sex, this treatment allows us to better interpret sex differences in environment-selection relationships. Specifically this model took the form;

$$\begin{aligned}\text{logit}(E[W]) = \alpha_B + B_1 z + B_2 z^2 + B_3 e + B_4 e^2 + B_5 \text{Sex} + B_6 ez + B_7 e\text{Sex} + B_8 e^2\text{Sex} \\ + B_9 z\text{Sex} + B_{10} z^2\text{Sex} + B_{11} ez\text{Sex} + b_t + \epsilon_i.\end{aligned} \tag{14}$$

This models how individual absolute survival data is related to the trait value, z, environment, e and sex, Sex, quadratic terms and relevant interactions are also included with residual error, ϵ_i. As temporal variation is being investigated the period between replicated selection events, t, in this case year, was included as a random variable. Since the residual variance is unobservable in a binomial model with a single trail per unit of observation, the residual variance was fixed to one (Morrissey *et al.*, 2014). Using the fixed factor coefficients of equation (14) we can construct a function to estimate absolute fitness of an individual, of either sex, with any trait value for a given environment condition in an average year;

$$\begin{aligned}W(z, e) = E\left[W|z, e, \text{Sex}\right] = \int_{-\infty}^{+\infty} g'\Big(\alpha_B + B_1 z + B_2 z^2 + B_3 e + B_4 e^2 + B_5 \text{Sex} + B_6 ez + eB_7\text{Sex} \\ + B_8 e^2\text{Sex} + B_9 z\text{Sex} + B_{10} z^2\text{Sex} + B_{11} ez\text{Sex} + \epsilon_i\Big) p(\epsilon) d\epsilon,\end{aligned} \tag{15}$$

where g' is an inverse logit function and $p(\epsilon)$ is a standard normal density function corresponding to the fixed overdispersion term evaluated at ϵ.

The dependence of mass on population size was modelled, again with year as a random variable, as

$$z_i = \alpha_C + C_1 e + C_2 \text{Sex} + C_3 e\text{Sex} + b_t + \epsilon_i. \tag{16}$$

Using the coefficients from this model we can construct a function predicting population mean mass from population size as

$$\overline{z}\,(e) = E\,[z|e, \text{Sex}] = \alpha_C + C_1 e + C_2 \text{Sex} + C_3 e\text{Sex}. \tag{17}$$

This allows the prediction of the mean trait value in any given environment. Finally we estimated the log of the trait variance and the standard error of that log variance individually for each year. We estimated the standard error of the estimates of the phenotype variance as $\hat{\sigma}^2_{zt}\sqrt{\frac{2}{N_t-1}}$ where N_t is the number of individuals of a given sex in a given year, this comes from the chi-square distribution of $S^2(n-1)/\sigma^2_{zt}$ with $n-1$ degrees of freedom. We obtained corresponding standard errors of log variances by the delta method (see e.g. Appendix 1 of Lynch & Walsh, 1998). These values were used to fit a model of how the trait variance changes with the environment, taking account of the errors in the variance estimates;

$$\log\left(\hat{\sigma}^2_{zt}\right) = \alpha_D + D_1 e_t + D_2 \text{Sex} + D_3 e\text{Sex} + m_t + \epsilon_t. \tag{18}$$

The measurement error associated with the log of the estimate of trait variance is included as m_t with a distribution $m_t \sim N(0, SE_t^2)$ and the residual error, ϵ_t, is distributed as $\epsilon_t \sim N(0, \sigma_t^2)$. The resulting coefficients can be used to construct a function for predicting $\sigma^2_z\,(e)$;

$$\sigma^2_z\,(e) = E\left[\sigma^2_z|e, \text{Sex}\right] = e^{(\alpha_D + D_1 e_t + D_2 \text{Sex} + D_3 e\text{Sex})}. \tag{19}$$

This allows prediction of the trait variance in a given environment.

Using the equations (15), (17) and (19), the mean fitness in a given environment can be calculated as the integral of absolute fitness as a function of the trait, z, and environment, e, $W(z, e)$, multiplied by the weighted probability density function of the trait in that environment, $p(z; e)$,

$$\overline{W}\,(e) = \int_{-\infty}^{+\infty} W(z, e) p(z; e) dz, \tag{20}$$

where $p(z; e)$ is a normal probability density function with the mean and variance determined by the envi-

ronment according to

$$p\left(z;e\right)=N\left(z;\overline{z}\left(e\right),\sigma_{z}^{2}\left(e\right)\right), \tag{21}$$

with $N(z;\bar{z}(e),\sigma_z^2(e))$ representing the density of a normal distribution with mean, $\bar{z}(e)$, and variance, $\sigma_z^2(e)$, evaluated at z.

The selection differential (equation 3) in any given environment can then be expressed as

$$S\left(e\right)=\frac{1}{\overline{W}\left(e\right)}E\left[zW\left(z,e\right)\right]-E\left[z\right]E\left[W\left(z,e\right)\right]=W^{-1}\mathrm{cov}\left(z,W\right)$$

and therefore,

$$S\left(e\right)=\frac{1}{\overline{W}\left(e\right)}\int_{-\infty}^{+\infty}zW\left(z,e\right)p\left(z,e\right)dz-\overline{z}\left(e\right)\overline{W}\left(e\right). \tag{22}$$

Calculating sensitivities

In a given environment, the sensitivity of the selection differential to the environmental variable is given by

$$\frac{dS\left(e\right)}{de}=\lim_{h\to0}\frac{S\left(e+h\right)-S\left(e\right)}{h}. \tag{23}$$

In practice, setting h to a small number, relative to the range of the environmental variable, allows the sensitivity of the selection differential to the environment to be accurately evaluated numerically. The average sensitivity of selection can be calculated as the sensitivity averaged over all observed values of e.

For the Soay sheep data, we calculated the sensitivity of the selection differentials to population size for the population size recorded each year with h set as 1. To quantify error associated with each estimate we repeated the analysis integrating over 1000 samples of the posterior distribution of the models specified by equations (14), (16) and (18), to generate posterior distributions of the average sensitivity of S to e.

Partial sensitivities

In order to establish how sensitive selection is to each of the four paths we have identified through which the environment can alter selection (Table 1, Figure 1), we can perturb the model defined by equations (22) and (23) according to the effects acting through each path. This requires that the perturbation, h in equation (23), can be broken down into the components relating to each path. We re-define h (see equation 23) as a vector,

$$\mathbf{h}=\left[h_{\mu},h_{\sigma^{2}},h_{a},h_{b}\right], \tag{24}$$

where the four vector components relate to the four paths:

h_μ - a change in trait mean,

h_{σ^2} - a change in trait variance,

h_a- a change in mean fitness, and

h_b- a change in the relationship between the trait and fitness.

Equations (15), (17) and (19) can be altered to include this **h** vector. With resulting set of equations we can predict the mean absolute fitness in any given environment while allowing manipulation of one of the four vector component pathways at a time, holding the others constant:

$$W(z,e) = E\left[W^*|z,e,\text{Sex},\mathbf{h}\right] = \int_{-\infty}^{+\infty} g'\Big(\alpha_B + B_1 z + B_2 z^2 + (B_3 + B_7\text{Sex})(e+h_a) + (B_4 + B_8\text{Sex})(e+h_a)^2 + B_5\text{Sex} + (B_6 + B_{11}\text{Sex})(z(e+h_b)) + B_9 z\text{Sex} + B_{10} z^2\text{Sex} - (B_6 + B_{11}\text{Sex})(\mu_c h_b) + \epsilon\Big) p(\epsilon) d\epsilon. \tag{25a}$$

$$\overline{z}(e) = E\left[\overline{z}^*|e,\text{Sex},\mathbf{h}\right] = \alpha_C + C_1(e+h_\mu) + C_2\text{Sex} + C_3(e+h_\mu)\,\text{Sex} \tag{25b}$$

$$\sigma_z^2(e) = E\left[\sigma_z^{2^*}|e,\text{Sex},\mathbf{h}\right] = e^{\left(\alpha_D + D_1\left(e+h_{\sigma_z^2}\right) + D_2\text{Sex} + D_3\left(e+h_{\sigma_z^2}\right)\text{Sex}\right)} \tag{25c}$$

The subtraction of $B_6(\mu_c h_b)$ from equation (25a) is an adjustment to correct for changes in the mean fitness that are a consequence of a change in the fitness function slope rather than a direct change, where μ_c is the result of equation (25b) when $h_\mu = 0$. The selection differential can then be calculated as

$$S^*(e,\mathbf{h}) = \frac{1}{\overline{W}(e)} \int_{-\infty}^{+\infty} zW(z,e,\mathbf{h})\, p(z;e,\mathbf{h})\, dz - \overline{z}^*(e,\mathbf{h})\,\overline{W}(e), \tag{26}$$

where

$$p(z;e,\mathbf{h}) = N\left(z; z^*(e,\mathbf{h}), \sigma_z^{2^*}(e,\mathbf{h})\right). \tag{27}$$

The partial sensitivities are then

$$\frac{\partial S^*(e)}{\partial e} = \lim_{h_j \to 0} \frac{S^*(e) - S(e)}{h_j}, \tag{28}$$

where h_j is the component of the **h** vector that is non-zero.

We averaged the partial sensitivities calculated at the observed population size each year over the observed population sizes to allow calculation of the average proportion of the total sensitivity that can be attributed to each of the fours components. As for the full sensitivities we integrated this analysis over the posterior distribution of the models specified by equations (14), (16) and (18), to generate posterior distributions of

each of the average partial sensitivities of S to e.

All analyses were carried out using the R statistical package (R Core Team, 2013) and all mixed models (equations 9, 10, 14, 16 and 18) were fitted using the MCMCglmm package (Hadfield, 2010).

Results

Regression of phenotypic selection coefficients on the environmental covariate

Estimated annual selection differentials of lamb August body mass are predominantly positive. For females the estimated selection differentials range from -0.397 ± 0.397 kg (estimate ± SE) in a year with a population size of 211 (1989) to 2.738 ± 0.426 kg where the population size was 671 (2004). In males the lowest estimated selection differential is -1.542 ± 1.542 kg at a population size of 211 (1989) rising to 2.187 ± 0.482 kg at a population size of 575 (1996) (Table 3). The selection differentials covary positively with population size in both sexes with strongest selection in years with higher numbers of individuals (Figure 2). The estimated regression slope is 0.004 kg sheep^{-1} (95% credible interval 0.003 - 0.006) for females and 0.006 kg sheep^{-1} (95% C.I. 0.003 - 0.008) for males.

The variance in selection attributable to variance in the population size is 0.488 (95% C.I. 0.153 to 0.831) for males and 0.274 (95% C.I. 0.097 to 0.497) for females. This means that the proportion of variance in selection explained by population size is 0.787 (95% C.I. 0.560 to 0.972) for males and 0.644 (95% C.I. 0.385 to 0.881) in females.

In contrast, if we had not accounted for the error in the selection coefficient estimates we would only have been able to attribute a proportion of 0.442 (95% C.I. 0.139 to 0.753) in the variation seen in selection in males to changes in population size and similarly only a proportion of 0.489 (95% C.I. 0.173 to 0.886) in females.

Model based full and partial sensitivities

Environmentally structured fitness functions for both sexes are depicted in Figure (3) modelled by equation (14); the coefficients from this model are shown in Table (2). In both sexes, lambs with a higher August mass have a better chance of survival. Individuals with low August mass have a greater likelihood of winter survival when born into a low population size than they would in high population years. Overall, female lambs (Figure 3B) are more likely to survive their first winter than males (Figure 3A). Their August mass has a greater influence on their winter survival than males, with lighter males showing less variation in survival across population sizes. The effect of mass on survival is more pronounced at large population sizes

in males, while at low population sizes (below 300) males survive well regardless of their phenotypes.

The relationship between mean lamb mass in August and population size modelled by equation (16) is shown in Figure (4). Mean August lamb mass is higher in years of low population size, with the difference being more apparent in males with a regression slope of -0.004 kg sheep^{-1} (95% C.I. -0.007 to -0.001) compared to -0.002 kg sheep^{-1} (95% C.I. 7.992×10^{-4} to -0.004) in females.

The relationship between the variance in lamb mass in August and population size is shown in Figure (5) modelled by equation (18). Variance in August lamb mass is slightly higher in years of high population size, with males having a regression slope of 2.009×10^{-4} kg^2 sheep^{-1} (95% C.I. -3.658×10^{-4} to 9.217×10^{-4}) and the slope for females being 2.371×10^{-4} kg^2 sheep^{-1} (95% C.I. -5.098×10^{-4} to 8.698×10^{-4}).

Mean absolute fitness ranges from 0.108 in years with high population size to 0.961 in years of low population size for males. Mean absolute fitness in females is consistently higher than in males ranging from 0.198 to 0.951 with the greatest differences between the sexes seen in years of high population size. The estimated mean absolute fitness for each population size observed in the data set are plotted in Figure (6).

The predicted environment-specific selection differentials for males range from -0.046 kg at the largest observed population size to 2.773 kg at the lowest population size. In females the range is from 0.041 kg to 1.902 kg. The estimated selection differential for each observed population size are plotted in Figure (7).

The average full sensitivity of selection to population size for males is 0.007 kg sheep^{-1} (95% C.I. 0.003 to 0.011) and 0.004 kg sheep^{-1} (95% C.I. 0.001 to 0.008) for females, indicating that the selection differential may be more sensitive to a change in population size for males than females. In females changes in the selection differential are largely driven by changes in mean fitness, with the partial sensitivity relating to mean fitness being 0.003 kg sheep^{-1} (95% C.I. 3.169×10^{-4} to 0.006). In males, this change is influenced by both the mean fitness, 0.003 kg sheep^{-1} (95% credibility interval 2.733×10^{-4} to 0.006) and the relationship between the trait and fitness, 0.003 kg sheep^{-1} (95% C.I. 0.002 to 0.005). The average full sensitivities and partial sensitives for both males and females are plotted in Figure (8).

Discussion

The absolute fitness function i.e. the relationship between unstandardised measures of phenotype and expected absolute fitness, is surprisingly rarely considered in studies of natural selection in the wild. When selection is characterised primarily via the relationship of traits with relative fitness (i.e. phenotypic selection coefficients) substantial information regarding variation in the selection may be lost. Consequently, any observed change seen when calculating multiple phenotypic selection coefficients is likely to be attributed to differences in the relationship between trait and fitness. However, this lost ecological information can be

retained if we study fitness functions and distributions of phenotype in conjunction with the measures of natural selection that are justified in evolutionary quantitative genetic theory.

The purpose of our illustrative example of these relationships (Table 1, Figure 1) is twofold. First, we wish to make it clearer and more widely known that there is a much richer range of paths through which biological variables could potentially explain any pattern observed in phenotypic selection coefficients. In fact, not only are there explanations that are typically ignored, but these explanations can act simultaneously. Two comparable replicates of selection could have the same values for selection differentials and gradients (i.e. selection has the same evolutionary effect) but there still be differences in the nature of the selection acting on the trait. For example, one replicate could have both a stronger trait-(absolute) fitness relationship, and higher fitness. In this case consideration of only the selection gradients would fail to reveal interesting aspects of the evolutionary ecology of the study system. Second, by putting these principles into a formal mathematical structure, the theoretical component of our work points the way to implementing estimates of fitness functions as part of formal methods for inference of selection. Previously known partial determinants of phenotypic selection coefficients including a population's mean fitness (Wade & Kalisz, 1990) and the distribution of phenotype (Wade & Kalisz, 1990; Steele *et al.*, 2011; Haller & Hendry, 2014; Chevin & Haller, 2014) have not, until now, been incorporated into approaches designed to increase understanding of variation in selection.

It is important to note that the fact that changes in mean fitness, and in the distribution of phenotype, can influence the values of selection gradients and differentials in no way invalidates the quantitative genetic theory by which selection gradients are justified. A change in the intercept of a linear fitness function, in the absence of changes in other relevant variables such as its slope and the distribution of phenotype, does cause relative differences in fitness among individuals to be less than they otherwise would. Correspondingly, we would expect the evolutionary consequences, e.g., predictions of the breeders (Lush, 1937; Falconer & Mackay, 1996) or Lande (Lande, 1979; Lande & Arnold, 1983) equations, of this lesser selection coefficient to be smaller than usually estimated. There has been substantial discussion of the importance of understanding the effects of ecological variables on the form of natural selection in the wild. However, the key point is that ways of establishing the consequences of these effects have not been fully integrated into theory, methods, and empirical studies of the variation of natural selection. Accordingly, methods have not previously been developed to study the pathways by which ecological variables might affect fitness variation.

From an ecological perspective, having an understanding of variation in absolute fitness (e.g. survival probability or reproductive success) under a fluctuating environment is crucial. Under a linear fitness function, as shown in Figure (1), when observed changes in selection are driven by an altered trait distribution the survival probability of an individual of a particular phenotype is not going to change with the environ-

446 mental variable. Therefore, knowing what is driving changes observed in selection differentials, and correctly
447 interpreting the consequences that this will have under the fitness model being used, provides an important
448 link between the fields of ecology, evolution and demography. By deriving information about variation in
449 selection from models of absolute fitness dependence on phenotype and environment, we are able to say more
450 about how population level metrics are affecting changes in selection. This type of information is highly
451 relevant to those studying demography in wild populations.

452 Our analyses were conducted using unstandardised phenotype values (apart from mean-centring across
453 the whole study) so as not to obscure any paths by which the environment may ultimately affect selection.
454 The principle of multiple pathways affecting phenotypic selection coefficients will hold for other coefficients,
455 including both gradients and differentials, under different standardisations. Therefore, the basic principle
456 that phenotypic selection coefficients can be affected by the environment via the four paths identified (Figure
457 1, Table 1) should hold regardless of the kind of selection coefficient or standardisation (with the exception
458 that an unstandardised selection gradient will be unaffected by changes in the trait variance, when a fitness
459 function is linear). However, this list of pathways is only exhaustive for cases of linear absolute fitness
460 functions and when the traits analysed are normally distributed.

461 Using the calculation of the proportion of selection explained by the environment in the regression-
462 based analysis (Figure 2) demonstrates a relatively easy way to produce a quantitative measure that can be
463 compared across studies. Use of a measure such as this could support meta-analysis of the environmental
464 dependence of selection that allow investigation of commonalities in links between environmental variables
465 and selection across study systems. In particular, the proportion of variation in selection explained by
466 the environment, when accounting for statistical noise in phenotypic selection coefficients estimates, will be
467 particularly useful. Other approaches will underestimate the strength of environment-selection relationships.
468 The proportion of variation in selection explained by the environment rises from 0.442 to 0.787 in males and
469 from 0.489 to 0.644 in females when the associated errors are considered.

470 Our model-based approach (equations 15, 17 and 19) to analysing the components of the total effects of
471 an environmental variable, population size, on viability selection of summer lamb mass in male and female
472 Soay sheep (Figure 8) revealed total effects of density similar to regression-based methods (Figure 2) that
473 characterise only the total effect. Selection of mass in both sexes is predominantly positive, and increases in
474 both sexes with population size. The model-based average sensitivity of selection to population size, 0.007
475 kg sheep^{-1} in males and 0.004 kg sheep^{-1} in females, matches reasonably well to the closely-related parameter
476 of the slopes of the linear regressions of selection differentials on population size, 0.006 kg sheep^{-1} and 0.004
477 kg sheep^{-1}, respectively. Changes in the mean (Figure 4) and variance (Figure 5) of mass in response to
478 population size are modest in both sexes. Consequently, effects of density on selection do not act through

these descriptors of the trait distribution (Figure 8). However, population size does substantially affect mean fitness (Figure 6, Table 2), and consequently, mean fitness is the main variable through which density affects selection in females (Figure 8), and a major contributor in males (Figure 8).

An important methodological consideration for studies of variation in selection based on inferences of environmentally-structured fitness functions, and effects of the environment on distributions of phenotype, is the nature of the component models (equations 25a, 25b & 25c in our analysis) in any such analysis. In particular, any component model predicting absolute fitness from values of phenotype and ecological variables will have to be sufficiently flexible. Main effects and interactions of phenotype and environment will generally be necessary while additional terms may add realism. If a study seeks to extend the basic analysis to understanding variation in quadratic selection, it will be necessary to include interactions of the environmental variable with non-linear terms pertaining to phenotype. Our choice of a generalised (specifically, using a binomial distribution) function for fitness was probably not necessary. In fact, in some situations, a linear model (i.e., not a generalised analysis) of trait-environment-fitness relationships could be most useful. The non-linear link functions used in generalised model induce a certain amount of dependence between the intercept and slope of fitness functions on the data (as opposed to the latent) scale. In our case, there will be little dependence, on average, because values of expected fitness take a large range and the dependence of the mean and slope on the intercept have opposite signs when expected fitness is above and below 0.5. When our analyses is carried out using a linear mixed model instead of the generalised fitness function (S2 in Supplementary Material) the results obtained are broadly similar. In other situations, this dependence could be problematic. For example, if a log-link model were used, there would be no direct dependence of selection on the model intercept (Morrissey & Goudie, 2016). This would not invalidate the approach, but further developments, or use of linear models to characterise fitness functions, would be necessary.

Analyses such as those we have implemented here, to separate the effects of a driver of selection acting through trait-fitness relationships, mean fitness, and the distribution of phenotype, are potentially applicable in a wide range of study systems. It would be particularly interesting if mean fitness proved to be a major contributor to variation in selection of a range of traits in different study systems. While changes in mean fitness, which may be driven by environmental stochasticity, can effect variation in selection, they cannot in themselves change the sign of selection. A lot of interest in variation in selection arises from a desire to characterise the prevalence of fluctuating selection (e.g. as an explanation for stasis, Bell 2010; Uyeda *et al.* 2011; Chevin & Haller 2014; Estes & Arnold 2007), any generality in the finding that mean fitness is a major driver of variation in selection could imply that fluctuations in selection in the wild are even rarer than the most recent analyses (i.e., Morrissey & Hadfield 2012) have indicated. Further work on the dependence of

selection on density could be particularly valuable. It seems likely that different pathways through which ecology could alter the dependence of selection on population density could have different eco-evolutionary consequences (Sæther *et al.*, 2016; Engen *et al.*, 2017).

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Table 1: Derivatives for the selection differential with respect each parameter which can alter its estimation

Absolute Fitness Component	Derivative of S with respect to the absolute fitness component	Change in parameter required to decrease S_σ or β_σ as depicted in Figure (1)(plot)
Mean Fitness, $\frac{dS}{da}$	$\frac{-\sigma_z^2 b}{(a+b\bar{z})^2}$	Increase(a)
Trait/Fitness Relationships, $\frac{dS}{db}$	$\frac{\sigma_z^2 a}{(a+b\bar{z})^2}$	Decrease(b)
Trait Mean, $\frac{dS}{d\bar{z}}$	$\frac{-\sigma_z^2 b^2}{(a+b\bar{z})^2}$	Increase(c)
Trait Variance, $\frac{dS}{d\sigma^2}$	$\frac{b}{(a+b\bar{z})}$	Decrease(d)

Table 2: Coefficients from the individual mean fitness model

	Regression Coefficients	95% Credible Interval	p-value
(A) Fixed			
Intercept	−0.889	(−1.736, −0.103)	0.030
Mass	0.311	(0.218, 0.404)	0.001
Mass^2	−0.005	(−0.027, 0.017)	0.634
Sex	1.107	(0.717, 1.577)	0.001
Population Size	−0.016	(−0.022, −0.010)	0.001
Population Size^2	0.000	(0.000, 0.000)	0.494
Mass·Population Size	0.002	(0.001, 0.002)	0.001
Sex·Population Size	0.005	(0.002, 0.008)	0.002
Sex·Mass	0.195	(0.057, 0.350)	0.008
Sex·Population Size^2	0.000	(0.000, 0.000)	0.584
Sex·Mass^2	0.025	(−0.011, 0.061)	0.172
Sex·Population Size·Mass	−0.001	(−0.002, 0.000)	0.152
(B) Random			
Year(variance)	2.362	(1.111, 3.973)	*NA*

Table 3: Selection differentials and standard errors for first year survival for each sex in each cohort of lambs born. When all individuals survive the selection differential is 0 and no associated standard error can be calculated. Where an NA is shown for the selection differential all individuals with a known August mass died that year. Other instances of NA are in years when there was only one survivor and no associated error could be estimated. None of these cases were included in the regression analysis

		Males				Females			
Birth Year	Population Size	n	Surviving Individuals	Selection Differential(kg)	Standard Error	n	Surviving Individuals	Selection Differential(kg)	Standard Error
1985	509	4	1	−5.97	*NA*	5	0	*NA*	*NA*
1986	211	4	4	0.00	*NA*	3	3	0.00	*NA*
1987	331	39	37	0.12	0.09	39	32	0.30	0.20
1988	457	22	2	−1.23	2.69	23	9	1.56	0.56
1989	211	4	3	−1.54	1.54	7	6	−0.40	0.40
1990	290	21	18	−0.47	0.28	32	29	0.27	0.15
1991	414	40	16	1.61	0.51	61	21	1.80	0.41
1992	321	32	26	−0.31	0.24	29	25	−0.01	0.16
1993	443	40	18	1.36	0.47	54	28	1.10	0.33
1994	435	25	1	−0.99	*NA*	34	9	0.97	0.39
1995	357	31	30	0.01	0.01	47	42	0.07	0.05
1996	575	68	19	2.19	0.48	54	25	1.22	0.40
1997	542	47	14	1.62	0.55	39	16	1.07	0.40
1998	591	44	1	1.54	*NA*	50	8	0.90	0.43
1999	325	42	34	0.14	0.23	43	41	0.01	0.01
2000	461	29	26	0.33	0.20	34	27	0.06	0.14
2001	651	42	0	*NA*	*NA*	52	6	1.90	0.66
2002	335	36	35	−0.05	0.05	32	30	−0.08	0.06
2003	494	47	42	0.13	0.14	60	55	0.08	0.10
2004	671	46	3	2.13	2.53	47	2	2.74	0.43
2005	405	18	9	0.43	0.51	28	17	0.30	0.34
2006	467	33	6	1.20	0.95	23	12	1.09	0.39
2007	447	50	28	0.93	0.32	56	34	0.86	0.27
2008	567	56	28	0.26	0.36	57	32	0.59	0.23
2009	617	52	20	1.63	0.38	48	27	0.84	0.29
2010	672	37	11	1.93	0.58	66	26	1.21	0.31
2011	649	41	1	2.67	*NA*	41	5	1.84	0.63
2012	362	23	22	0.03	0.03	32	30	0.16	0.12
2013	545	47	8	1.86	0.54	50	13	0.83	0.72

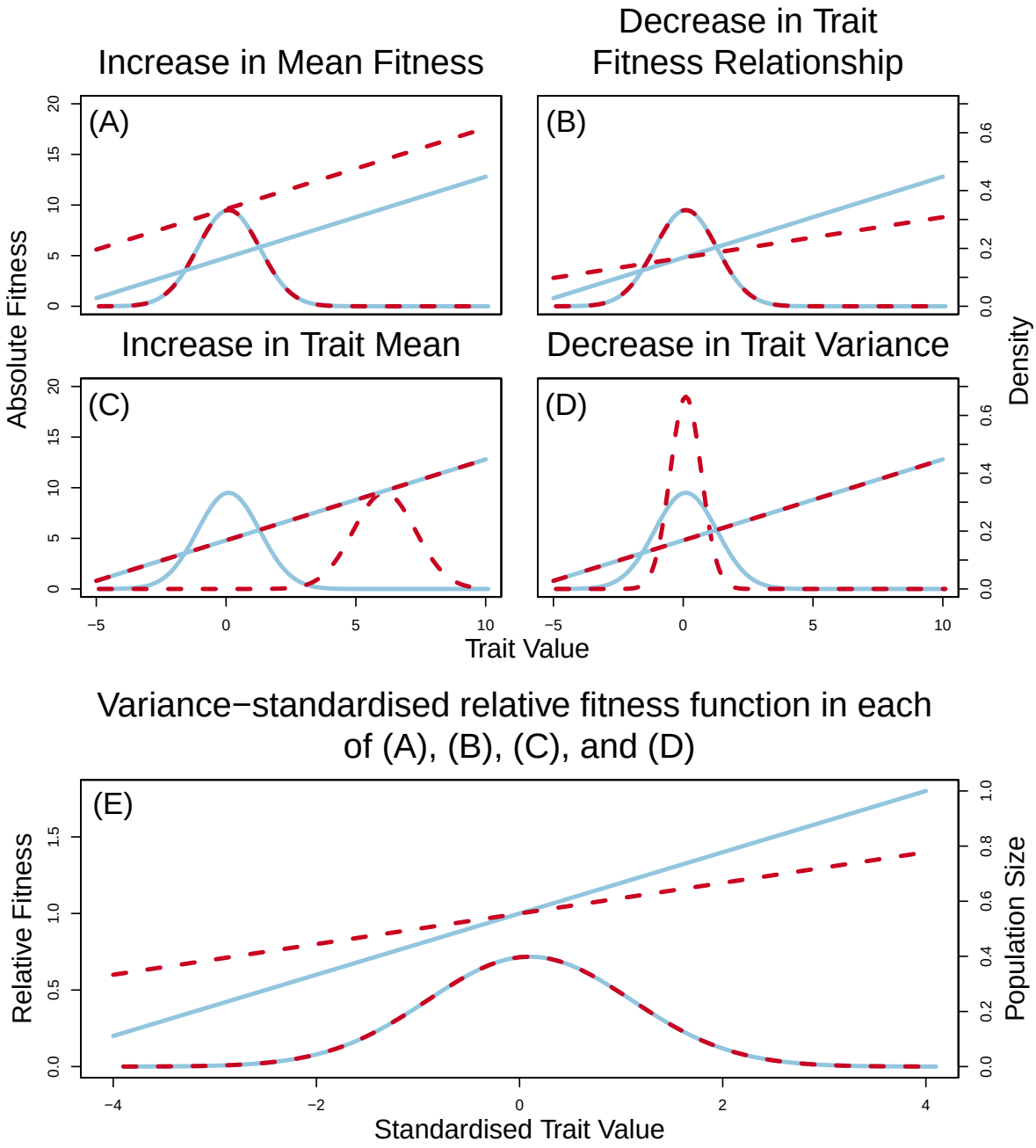

Figure 1: Graphs illustrating the fitness function change when only a single parameter of the trait to absolute fitness relationship, or distribution of phenotype, is altered. The trait values are related to absolute fitness using a linear fitness function. The resulting absolute fitness function is shown in the top four panels. In each case the solid blue line shows the same trait distribution and absolute fitness function while the dashed red line shows the effect of changing only the single parameter indicated above each graph. The bottom plot shows the resulting relative fitness function change when the trait values are mean centred and variance standardised. Importantly in each case illustrated in the top four plots the change in the variance-standardised selection slope, β, is the same despite very different underlying causes.

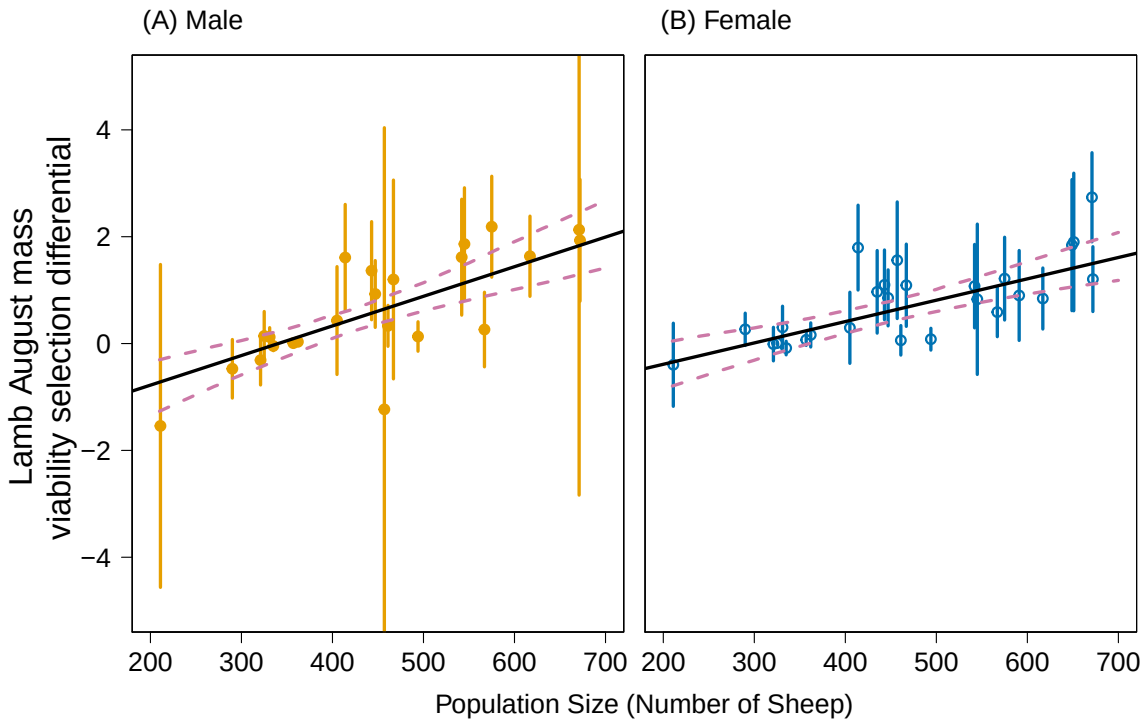

Figure 2: Regression of selection differentials on population size. Graphs showing the change in selection differentials for lamb mass in August with population size. The calculated selection differentials for male (A) and female (B) sheep are shown at different population sizes. The regression lines are calculated using a MCMCglmm model taking into account error in the estimates using their standard errors. The error bars show 95% confidence intervals assuming a normal distribution. The dashed lines show the 95% credibility regions for the regression lines. The slopes for males and females were not significantly different from one another.

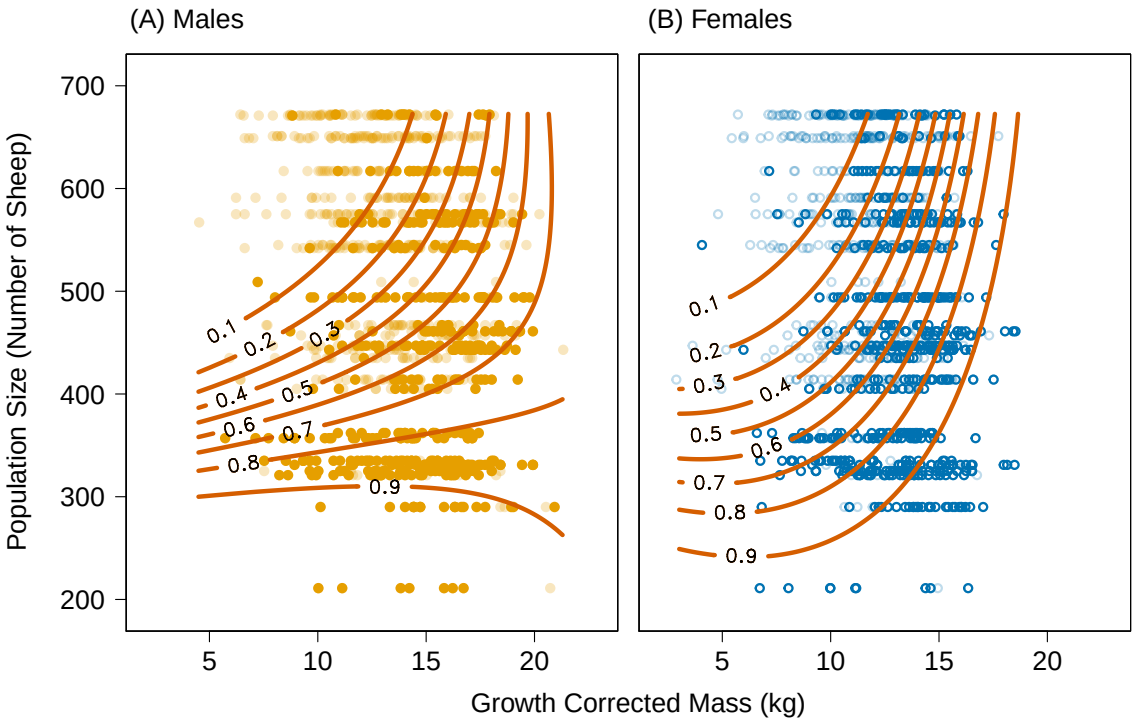

Figure 3: Environmentally Structured Fitness Functions. August mass of male (A) and female (B) sheep are shown at different population sizes. Realised survival is represented using points with higher transparency to represent individuals that did not survive their first winter. Fitness isoclines, showing the survival probabilities, are plotted using the intercepts and fixed factor coefficients shown in Table (1). In both sexes in years of low population size a much larger number of individuals are in the higher area of the fitness function meaning those with lower mass have a better chance of survival than they would in years of large population size. The apparent reduction in fitness at high mass and low population size seen in males compared to less extreme values is almost certainly due to limited data at the extremes of the dataset

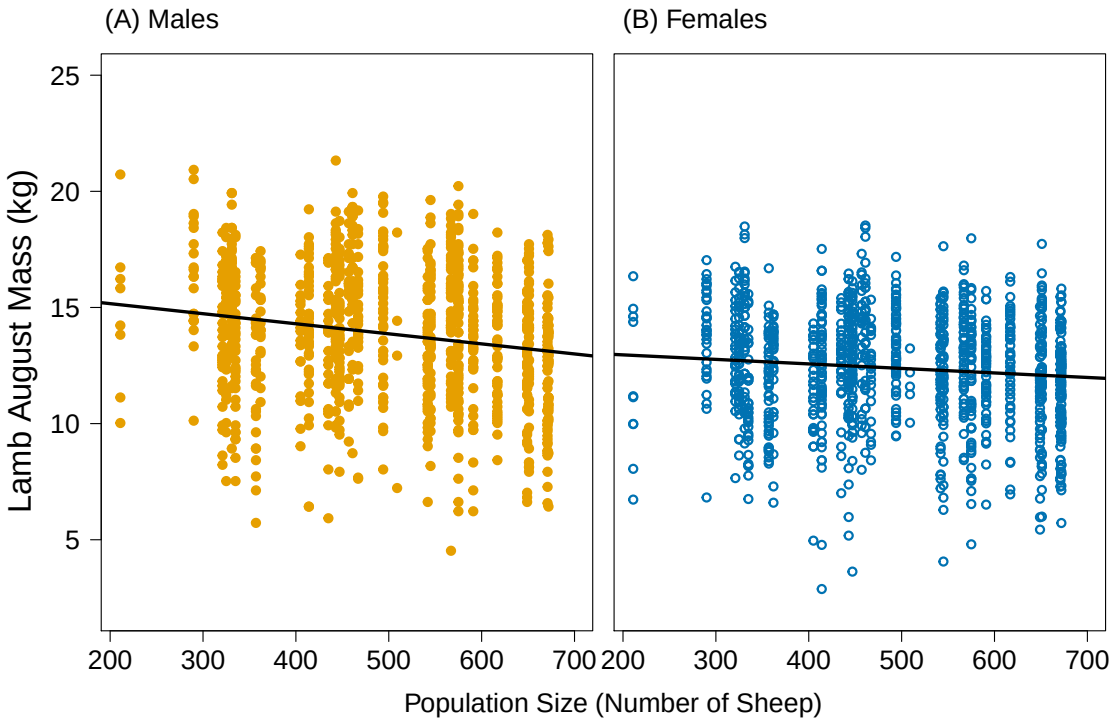

Figure 4: Regression of August mass on population size. August mass of male (A) and female (B) sheep are shown at different population sizes. Regression lines are plotted using the intercept and fixed-effect coefficients from applying equation (16)

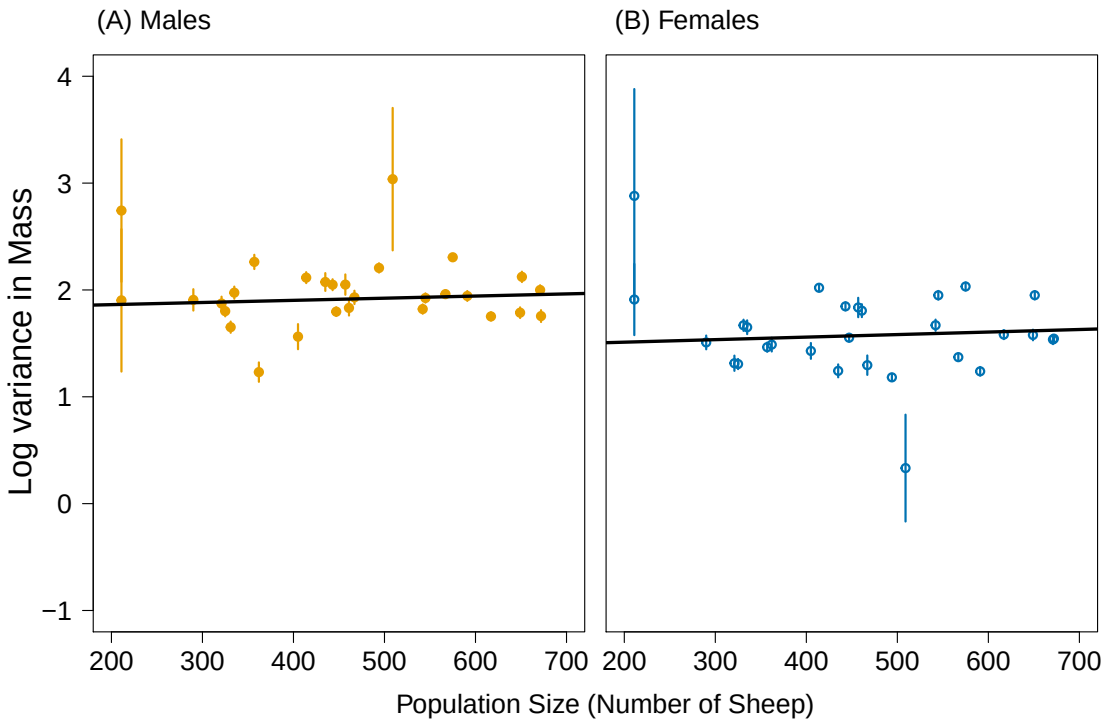

Figure 5: Regression of August mass variance on population size. The variance of August mass in male (A) and female (B) sheep are shown at different population sizes. Regression lines are plotted using the intercept and fixed-effect coefficients from applying equation (18). Error bars show the 95% highest posterior density interval.

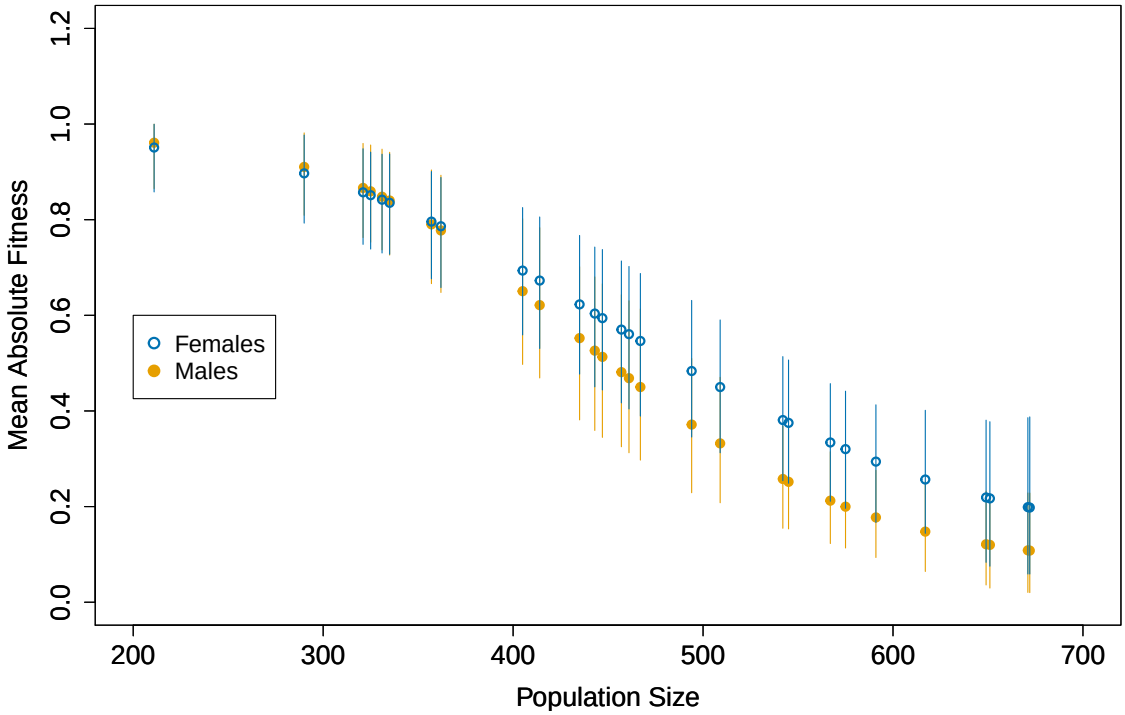

Figure 6: Mean absolute fitness against population size. Mean absolute fitness of male and female sheep are shown at different population sizes as predicted by our environmentally structured fitness function (equation 20)

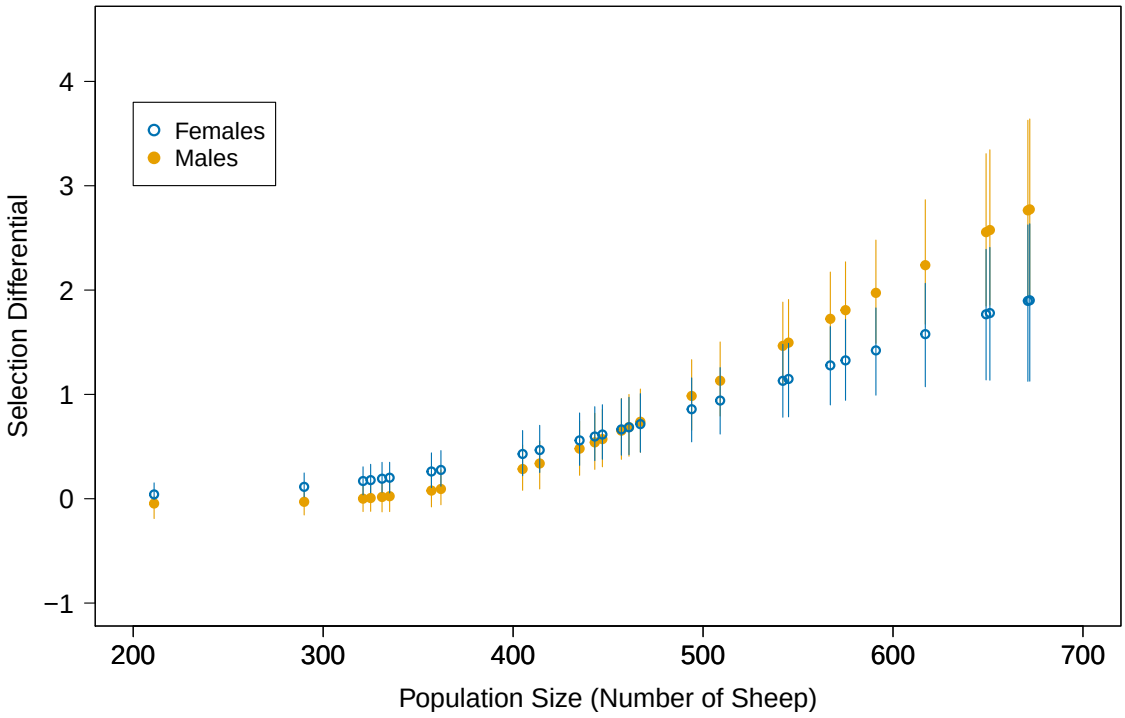

Figure 7: Selection differentials against population size. Selection differentials for male and female sheep are shown at different population sizes as predicted by our environmentally structured fitness function (equation 22)

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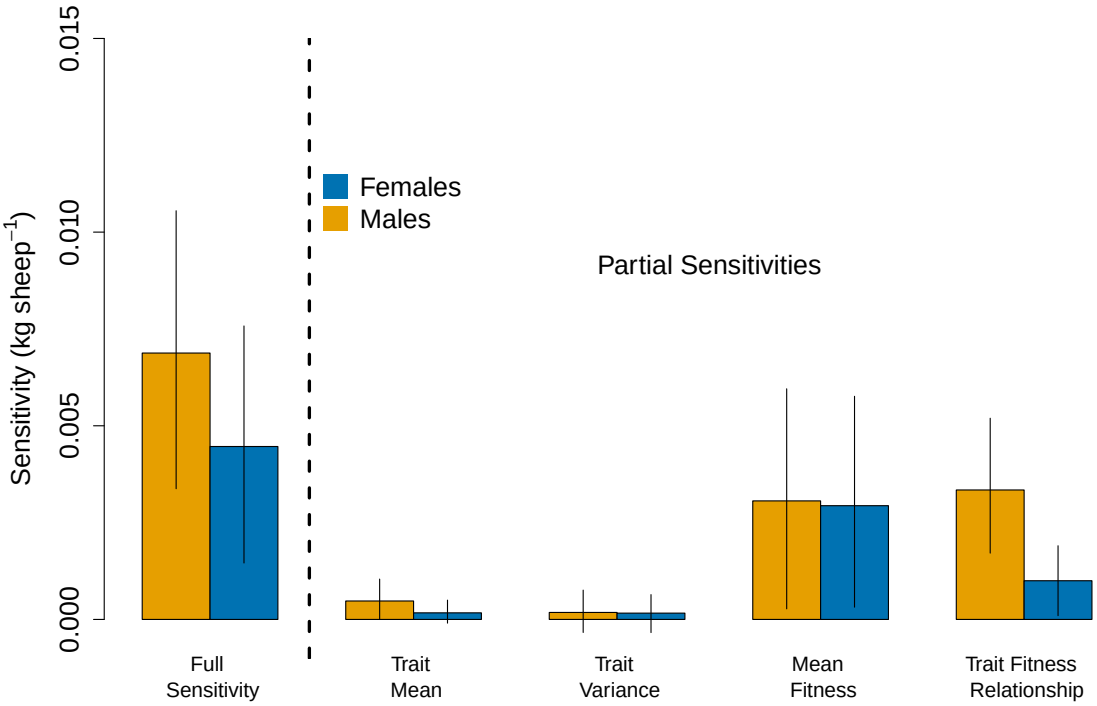

Figure 8: Full and partial sensitivities. The full and partial sensitivities are shown for male and female sheep. The partial sensitivities show the contribution of each of the four different pathways through which ecology can alter selection estimates.